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NOTES AND LITERATURE

HEREDITY

A SUBJECT of vital importance to the theory of heredity is the behavior of the chromosomes during the life history of the cell, and especially during the process of cell division. This subject has received an enormous amount of attention from investigators but there is far from unanimity amongst cytologists as to the actual phenomena of cell division, not to mention the significance of these phenomena. Realizing that the heterotypic division in gametogenesis is the critical point in the life history of the organism, so far as the theory of heredity is concerned, attention has been concentrated very largely on this division. This is in some respects unfortunate. A good many investigators who have studied this division have attempted to interpret the phenomena observed without full knowledge of the behavior of the chromatic elements in ordinary somatic divisions, and have attributed to phenomena observed in the heterotypic division very special meaning for inheritance, when these same phenomena are regular occurrences in all divisions, and hence are to be interpreted in their relation to growth rather than to reproduction.

The writer is not a cytologist, and realizes fully that his opinions on cytological questions will not be regarded seriously, especially by those who have worked at problems of this character until they have gotten fixed in mind certain theories as to the meaning of the phenomena observed. Nevertheless, he has given careful attention to published results of investigations of this character, and has been driven by study of these results to a particular interpretation of the principal phenomena reported. It has seemed to me for some years that the double spireme so often reported in the heterotypic division, and so often interpreted as a conjugation of homologous chromatin elements, although this double spireme occurs in somatic divisions, apparently quite as generally as in the heterotypic, is nothing more than the expression of a division of chromosomes which really occurs at least as early as the resting stage following the previous nuclear division. It appears that this division may begin at an even earlier period.

Fraser and Snell, in their paper on "The Vegetative Divisions in *Vicia faba*,"[1] present important evidence on this point. They show very clearly that the division begins in the teleophase of the previous division. This beginning of chromosome division in teleophase had earlier been noticed by Gregoire, and by Stromp, as pointed out by Fraser and Snell, but these earlier investigators had not perceived the meaning of this phenomenon. Fraser and Snell were able to follow the life history of the chromosomes through their complete history from one teleophase to the next (in root tips and in other somatic parts, as well as in the gametophyte stages), and they show clearly that the double nature of the spireme is due to splitting which begins as the daughter chromosomes congregate at the poles in the teleophase of the previous nuclear division.

That this double spireme is not due to the approximation of two elements, one representing maternal and the other paternal chromatin, is further shown by the fact that in the pollen cell, where the chromosome number is haploid, and hence where there can be no question of union of elements from the two parents, exactly the same phenomena occur.

Another very interesting fact shown by these investigations (of Fraser and Snell) is that some of the elements which behave as single chromosomes, so far as their distribution on the spindle and to the poles is concerned, are made up of segments united end to end, as if two or more small chromosomes were united more or less closely into a larger one. The authors point out the possible significance of this fact for Mendelian coupling, and suggest that it may also be of significance in connection with the fact that in some species more Mendelian factors have been observed than there appear to be chromosomes.

East and Hayes have recently published the results of extended investigations on inheritance in maize.[2] After discussing the taxonomy of the group and pointing out the adaptability of maize to genetic investigations (or the lack of such adaptability), the authors give an excellent résumé of former investigations with this interesting group of plants.

A brief account of their results follows. Amongst endosperm characters they found that starchiness (S) is dominant to its absence, non-starchiness (*s*). When *S* came from the ♂ parent zenia appeared in all cases. All F_1 seeds showing zenia proved to be heterozygous. No extracted recessives of the F_2 generation ever proved to be heterozygous. "From this one may conclude that the second male nucleus that fertilizes the endosperm nucleus always bears the same characters as the first male nucleus that fertilizes the embryo nucleus, or egg." A few seeds, all heterozygous, were part starchy and part not; *i. e.*, one side was starchy. The authors consider that this confirms Correns's view that, in such cases, the second male nucleus did not fuse with the endosperm nucleus but that each developed separately.

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[1] *Ann. of Bot.*, 1911, pp. 845–856.

[2] E. M. East and H. K. Hayes: Bul. No. 167, Conn. Exp. Sta.—"Inheritance in Maize."

One semi-starchy ear occurred, grown from a non-starchy seed. The authors suggest two possible causes for this phenomenon. Either there is an incomplete segregation, resulting in contamination of a gene by its allelomorph, this contamination, by selection, being capable of accumulative effects, or the semi-starchy ear arose as the result of a progressive variation. They point out that the infrequency of this phenomenon is an argument against the theory of partial or incomplete segregation, and incline to the idea that it is a case of progressive variation. The data presented certainly favor this interpretation of the case.

YELLOW AND NON-YELLOW ENDOSPERM

Two independent factors for yellow were found, each capable of producing yellow endosperm. The colors produced by these two factors appear to be the same. The pigments occur in rhombic plates, and are insoluble in water, but soluble in ether, chloroform, etc. They appear to be related to the anthochlorins.

Some crosses between yellow and white gave the ratio 3 : 1, due to the presence of only one of the factors for yellow. Others gave the dihybrid ratio. Yellow appeared as xenia in the hybrid seeds (seeds which produced the F_1 plants).

Yellow was dominant, but imperfectly so under certain conditions, so that, in certain crosses in which the grains had soft starch at the tip the heterozygotes could be distinguished from the homozygotes. In other crosses yellow was completely dominant.

The same original ear of some of the parent stocks had some seeds containing both factors for yellow, while other seeds on the same ear had only one of these factors.

The two yellow factors together generally gave darker yellow seed than one factor alone.

Purple and Non-Purple Aleurone Cells

The experimental data relating to crosses between purple and non-purple races indicate two factors, *P* and *C*, which, when together, produce purple color in the aleurone layer. In some of the non-purples used one of these factors was missing, in others both. In certain combinations one of these factors alone produced faintly colored purple. In most of the crosses splashed purple occurred, part, but not all, of the heterozygotes having this peculiarity. It was not hereditary, but behaved in subsequent generations as pure purple.

In one family red aleurone occurred in F_2. It appeared to be due to the interaction of two factors *R* and *C*.

In one family of this cross (purple × non-purple) the F_2 generation gave purples, reds, and non-purples in the ratio 12:1:3. The actual numbers were 1,843:188:545. The ratio 12:1:3 did not occur in F_3, but instead one fifth of the ears bearing F_3 grains gave the ratio 9:3:4. Several possible hypotheses to explain these anomalous results are discussed and discarded, amongst them Bateson and Punnet's hypothesis of the formation of gametes in the ratio $7AB : 1aB : 1Ab : 7ab$. The data from F_3 agree best with the assumption that the constitution of the two parent types was *pcR* and *PCR* respectively, but the F_2 ratio is not explained by this hypothesis. The authors leave the question as to the real explanation an open one. The reds in this family were different in color from the reds of the family previously mentioned. Not only that, but all the F_2 reds found in this family proved to be homozygous, indicating that both parents possessed the factor *R*.

Other families of this cross gave results that indicated the presence in the non-purple parent of a factor which more or less completely inhibited the development of purple. Some nonconformable results were found, due probably to the presence of other factors, one at least of which appeared to modify purple by making it lighter.

In the above crosses xenia was found as follows: when non-starchy races were fertilized by pollen from starchy races (no xenia appeared in the reciprocal cross); when non-yellow endosperm is crossed with yellow endosperm. In this case xenia always appeared when yellow was used as the male parent. It also appeared in the reciprocal cross when the grains of the female parent had extensive development of soft starchy endosperm at the end of the grain, as in these cases the heterozygous yellow was lighter in color than the homozygous, and hence distinguishable from it. In crosses between yellow and non-yellow endosperm, when the non-yellow endosperm was entirely soft (not corneous), as in the so-called flour corns, xenia appeared in all cases, for reasons just stated. When the endosperm of the non-yellow parent was entirely corneous, as in the popcorns, xenia usually occurred only when yellow was used as the male parent, though in a few instances it was perceptible when the cross was made the other way. Xenia also occurred when purple or red aleurone was crossed with non-purple, or non-red, when the purple or red was used as the male. The only other case in which xenia was observed was in crosses between white and red (or purple) when the white (male) parent carried an inhibiting factor for purple and red. Sometimes the reciprocal cross shows xenia, since the inhibition of red or purple is not always complete. The following law regarding xenia is formulated by the authors: when two races differ in a single visible endosperm character in which dominance is complete, xenia occurs only when the dominant character is the male; when they differ in a single visible endosperm character in which dominance is incomplete or in two characters both of which are necessary for the development of the visible difference, xenia occurs when either parent is used as the male.

Correns's conclusion that where xenia occurs the seeds showing it are always hybrid is confirmed. This shows that Mendelian segregation must occur previous to the division of the pollen nucleus. The authors found no case in which a seed showing no xenia where it is to be expected proved to be a hybrid; *i. e.*, the hybrid in which xenia is to be expected always showed xenia though like Webber and Correns they found seeds showing xenia on only one side. This is interpreted as the result of the independent development of the endosperm nucleus and the second male nucleus.

In crosses between podded maize (maize having each grain covered by husks) with common maize, the pod character proved to be a dominant Mendelian factor, which segregated perfectly in F_2.

Red sap colors appear in maize in the pericarp, the cob, the husks, the silks, the glumes, and in the anthers.

Red pericarp (*R*) without red on the cob or in the silk, crossed with white pericarp gave three reds to one white in F_2, the segregation being perfect.

An ear of corn was found where only white corn had been planted, one side of which produced grains with red pericarp, the other white or striped with red. The red here seemed to be due to the same factor as in the case just noticed (R). Red grains from this ear gave red and white ears in equal numbers. The white and striped grains gave white ears and ears with a few striped red seeds in equal numbers. A selfed red ear in this generation gave three reds to one white in the next. The original red and white (or striped) ear is accounted for as a somatic variation, part of the ear varying from white to red, the remainder from white to striped. In this family red cob is perfectly correlated with red pericarp.

Two other red pericarp colors, apparently independent of the above, were found. One is a dark red occurring in stripes which radiate from the point of the attachment of the silk to the grain. The other is a dirty red, more abundant at the base of the grain, and nearly wanting at the tip. It occurs in Palmer's Red Nosed Yellow variety. It is completely coupled with red silks.

Two other red pericarp factors were found. They are very similar, but not allelomorphic to each other. They give a rose red pericarp, but do not develop except in sunlight. They are barely perceptible on ears covered by heavy husks.

Red cob color proved to be dominant to white and the cross segregated in a 3:1 ratio. Red cob appears not to be correlated with any of the red pericarp colors.[3]

Red silk color presented some difficulties, and the data are not analyzed. In some instances a 3:1 F_2 ratio was obtained, in others a third type with red hairs on a greenish-white silk occurred, the F_2 numbers being 198 reds, 29 greenish-whites with red hairs, and 94 greenish-whites. Red silks may occur with no other red on the plant.

Red glumes were always accompanied by red in other parts of the plant, though in one race the only other red was in the silks.

The question whether all these reds are due to one or to different genes is discussed most interestingly (pp. 109–10), but the discussion is too long to quote here.

It is gratifying to note that these authors are not afraid to mention the chromosomes in connection with Mendelian factors. For several years an inexplicable obsession seems to have possessed biologists in this matter. Apparently every one regards it as highly probable that these cell organs are in some way responsible for Mendelian phenomena, yet a large number of biologists seem to be afraid to refer to them in this connection.

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[3] But see reference to Emerson's results below.

Crosses between flint and dent varieties indicated that the difference between these two classes relates to two factors in some case, especially when the dent parent has considerable corneous endosperm, and to two or more factors, especially when the dent parent has little corneous starch. This seems to be another case where several similar factors exist, as found in earlier investigations by East, by Nilsson-Ehle, and by Shull.

Crosses between races having different modal numbers of rows of grain on the cob indicate clearly that several similar factors are here concerned. The evidence that segregation occurs is, the authors believe, conclusive. The data could not be definitely analyzed because of the fluctuating variation of the various biotypes, and the small differences between adjacent biotypes. Height of stalk and length of ear behave similarly. Apparently size of grain does the same.

Irregular rows of grain occur both as fluctuations not inherited and as a hereditary characteristic. Should the percentage of irregular rows be higher than about 4 per cent. the authors think the irregularity is probably hereditary.

This paper closes with a discussion of the inheritance of various abnormalities found during the progress of the work.

The *Journal of Genetics* for August, 1911, contains some articles of unusual interest. R. N. Salaman presents the results of an investigation on the inheritance of the peculiar physiognomy known as the Jewish face. He shows that this is a simple Mendelian character. It is distinctly recessive to the ordinary European (Gentile) physiognomy, though the hybrids sometimes show traces of the Jewish face, especially late in life. On the other hand, this peculiarity is dominant over the Pseudo-Gentile face sometimes seen amongst the Jews; also to the Gentile physiognomy of the Moors and certain other Mediterranean peoples. We may explain this in terms of the presence-absence hypothesis by saying that the distinctive type of face seen amongst the Hebrews is due to the presence of a gene, while in the peoples of northern Europe there is a gene which inhibits the Jew face character. The data presented, while not extensive, seem to be quite conclusive that the character segregates as a so-called unit character. Salaman's paper is an exceedingly clear presentation of data, and is written in a style that is attractive and readable.

Bateson and Punnett[4] give the results of their study of the inheritance of the peculiar black pigmentation in the skin, periostium, and other tissues of the silky fowl. While some exceptions occur, the results on the whole are in agreement with the assumption of a pigment factor, *P*, and an inhibiting factor *I*, the latter exhibiting the phenomenon of spurious allelomorphism with the female sex factor. The authors suggest that the exceptions found may be due to failure of the repulsion supposed to exist normally between the female sex factor and the inhibiting factor, *I*.

While a large part of the work on which Mendel's principles of heredity depend has been done with pigments, very few investigations have been undertaken in order to determine the connection between the phenomena of inheritance of these pigments and the chemical reactions which underlie these phenomena. This is quite natural, since few of those who have conducted the investigations relating to Mendelian inheritance have had the training, and hence the opportunity, to study the chemical side of the question. Likewise, those relatively few individuals who have become well versed in the highly complex and difficult subject of physiological chemistry have seldom had any direct interest in the phenomena of inheritance. The wisdom of an endowment for an all-sided research of heredity such as the Carnegie Institution of Washington has provided at Cold Spring Harbor is manifest in the fact that Dr. Davenport has been able to institute research on both sides of the question. The results secured by Mr. Gortner in his study of the origin of melanin, and its relation to the phenomena of Mendelian inheritance will be eagerly read by students of Mendelism. In the May number of the *Journal of Biological Chemistry* Mr. Gortner gives some exceedingly interesting results of his work. He shows that the body filling of the meal worm (*Tenebrio moliter*) contains two oxidases, a laccase-like enzyme, and a powerful tyrosinase. Also that there is a chromogen present in the larva which, when acted upon by the tyrosinase, gives a series of colors ending in a black melanin-like body. Larvæ killed by ether developed pigment when left exposed to air, but when the air was excluded by carbonic acid or nitrogen no pigment developed. When the larvæ were heated (in water) sufficiently to destroy the activity of the tyrosinase but not that of the laccase, no pigment formed.

The oxidase was evidently present in relatively large amounts, but the chromogen only in small quantities. The results indicate that the chromogen is formed slowly and used as formed.

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[4] *Jour. of Gen.*, Aug., 1911, pp. 185–203.

In the September number of the same journal[5] the same author deals with the nature of dominant and recessive white. He shows that, in so far as the presence or absence of pigment is concerned, these two types of white, in certain mammals, are as indistinguishable to the chemist as they are to the breeder. He accepts the view that pigment is formed by the action of an oxidase on a chromogen, and points out that dominant white arises from the presence of a third body which prevents the reaction between the oxidase and the chromogen. This might occur in three ways: (1) the third substance, such as orcin, resorcin, phloroglucin, or other substances of similar nature, may act on the chromogen and thus prevent its oxidation; (2) it may itself be oxidized by the tyrosinase, thus preventing action on the chromogen; (3) it may act as a true anti-oxidase, and in some manner inhibit the action of tyrosinase.

The author gives abundant data to show that alternatives 1 and 2 are excluded in the cases with which he worked. Hence the action must be of the third type—an inhibitory action. He shows that dominant whites contain no pigment lacking in recessives. He also shows that "aromatic compounds which carry two hydroxyl groups in the meta position to each other are capable of inhibiting the action of tyrosinase on tyrosin." If, then, such a substance should occur in the animal body a dominant white would result. Recessive white is presumably due to the absence of either the chromogen or the oxidase, while at the same time no inhibiting factor is present. From this it would appear that an albino might be dominant to color if it carried the inhibiting factor, yet it would require considerable work to distinguish between such an albino and a true dominant white, *i. e.*, by its genetic behavior.

To explain the occurrence of recessive whites which are not albinic, and which are dominant in some crosses, we have the following considerations. Orcin inhibits the action of tyrosinase on tyrosine, but is itself oxidized by a specific enzyme. If we represent tyrosine by C, tyrosinase by T, orcin by O, and the specific enzyme which oxidizes orcin by P, then an individual containing only C and T would be colored, CTO would be white, the cross $CTO \times CT$ would be white (*i. e.,* white would be dominant), the cross $CTO \times CTP$ would be colored (white recessive), while the cross $CTO \times TP$ (both white) would be colored.

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[5] R. A. Gortner: "Studies on Melanin: III. The Inhibitory Action of Certain Phenolic Substances upon Tyrosinase." *Jour. of Biol. Chem.*, Vol. X, No. 2, Sept., 1911.

It appears, therefore, that Gortner has been able to construct a theory that renders intelligible the behavior of all kinds of white color in inheritance, and to give what seems to be a very plausible chemical explanation of all these cases. We, of course, already understand why the cross of two whites of types Ct and cT should give color and why both of the latter types of white are recessive to color.

Readers of the NATURALIST are familiar with my contention that in order to show that the chromosomes, as a whole, are not responsible for Mendelian characters, it must be shown that more *independent* dominant characters can be put into a single individual than there are pairs of chromosomes. The fact has been repeatedly cited that more Mendelian characters have been found in *Pisum* than there are pairs of chromosomes, and the claim is made that this disproves the chromosome theory of Mendelism. I have repeatedly shown that this is not the case. There might be a thousand Mendelian characters demonstrated for *Pisum,* but until it is shown that more than six of them are genetically independent, the chromosome theory is not affected thereby. It has heretofore been *assumed* that two factors, each of which when crossed with its absence behaves as a so-called unit character, are genetically independent of each other. This assumption appears to be involved in the "presence-absence" hypothesis. This hypothesis, as usually applied, seems to imply the presence or absence of a particular *body* in the cell, which body, when present *once,* passes into only one gamete, and that there are as many such genetically independent bodies as these are Mendelian factors. When correlation of Mendelian factors occurs, it is assumed to be due to the adhering together of twc of these bodies; likewise when the so-called spurious allelomorphism occurs, it is because two of these bodies *repel* each other.

I wish here to repeat what I have often said before, that the fact that two factors each behaves as an allelomorph to its absence *does not prove them to be genetically distinct.* The occasion for this repetition is some pertinent evidence which has just been presented by some exceedingly interesting work of Professor Emerson's.[6] He found that red cob (with white pericarp)

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[6] R. A. Emerson: "Genetic Correlation and Spurious Allelomorphism in Maize." 24th An. Rep., Nebr. Agric. Exp. Sta., pp. 59–90.

× absence of red gives the usual Mendelian phenomena of 3 red cob : 1 white in F_2. Likewise, the cross red pericarp (with white cob) × absence of red gives 3 red pericarp : 1 white. Thus each of these types (factors) behaves as an allelomorph to its absence. Hence they should be due to genetically independent genes. But such is not the case; they are allelomorphic to each other.

Some students would say that this is because they *repel* each other. But this explanation does not satisfy in this case, for it can hardly be doubted that red cob in the one case and red pericarp in the other are due to the same cause, acting differently in the two cases. I am of opinion that many similar cases of factors behaving as allelomorphs to their absence will be found to be also allelomorphic to each other. Such cases have usually not been looked for. Quite a number of them have been reported, and I hope some time to be able to bring them all together for reference. Emerson[7] gives a case in beans, in which a variety with green leaves and green pods was crossed with another having green leaves and yellow pods. F_2 consisted of three of the former to one of the latter. Here green was allelomorphic to absence of green. Later he crossed two varieties, one with green leaves and green pods, the other yellow leaves and pods. F_2 consisted of three of the former and one of the latter. Here green was again allelomorphic to its absence. These two crosses apparently show that yellow pods with green leaves and yellow pods with yellow leaves are not genetically distinct. Yet if yellow had been dominant in both these cases, it would have been the usual custom to consider that the two different yellows were independent genetically, because each was allelomorphic to its absence. It would be interesting to know how the two yellows would behave if crossed. It would not be at all surprising to find these two "absences" exhibiting the phenomenon of spurious allelomorphism. The case would be still more interesting if a variety could be found with yellow leaves and green pods.

W. J. SPILLMAN

(*To be continued*)

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[7] *L. c.*